Turk J Bot
32 (2008) 433-446

Biogeography of South-West Asian Bryophytes – With Special Emphasis on the Tropical Element

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Received: 17.09.2008
Accepted: 27.10.2008

Abstract: The recent bryophyte flora of South-West Asia is heterogeneous and consists of 6 floral elements [(Sub)cosmopolitan taxa, northern taxa, xerotherm-Pangaean taxa, circum-Tethyan taxa, tropical taxa, and endemics of various origins] that are derived from the different Pangaean ancestral floral stocks. Analysis of the flora and vegetation indicates that there is a very strong tropical – and especially palaeotropical and Afromontane – influence in the bryophyte flora of the area. Altogether, more than 95 taxa, or nearly 10% of South-West Asia's total known bryoflora, are of xero-tropical origin. They concentrate mainly in the escarpment mountains of the Arabian Peninsula and Socotra Island, and often are unique relicts of a former wider distributed Tertiary xero-tropical flora that today links South Arabia with East Africa and South-East Asia.

Key Words: Chorology, circum-Tethyan, floral history, liverworts, mosses, xerotherm-Pangaean

Introduction

Within the evolution of the bryophytes, one can distinguish 2 outstanding phases, which in connection with plate tectonic processes are of decisive significance for all biogeographical considerations. Bryophytes originated in the Lower Devonian c. 350 million years ago. Already at the end of the Permian period, the major groups of Marchantiophyta (the former Hepaticae) and Bryophyta (Musci) were evolved and are represented by today's evolutionary lines (Frey, 1977; Oostendorp, 1987; Heinrichs et al., 2007). After this 'macroevolution' and the differentiation of the major groups in the Mesophyticum, no major evolution of new higher-ranked categories took place (Oostendorp, 1987). In the Late Cretaceous, however, one can observe a 'co-evolution' with angiosperms and a great diversification of the most derived and 'modern lines', such as Jungermanniales (e.g., Lejeuneaceae) and pleurocarpous mosses (e.g., Hookeriales and Hypnales) (Schuster, 1981).

Floral (geno-) Elements

The known fossils and the evolutionary data, as well as palaeohistorical and palaeogeographical data indicate 4 ancient pre-angiospermian distribution patterns of the bryophytes on a former supercontinent, called Pangaea (Frey & Kürschner, 1983, 1988; Frey, 1990) (Figure 1). These patterns include:

- Taxa with a northern Pangaean distribution, including the ancestors of the later Laurasian element.
- Taxa with a 'continental' Pangaean distribution = the later xerotherm-Pangaean and circum-Tethyan element (1 and 2 in Figure 1).
- Taxa with a southern Pangaean distribution, including the ancestors of the later Gondwanalandic element.
- Taxa with a nearly cosmopolitan Pangaean distribution.

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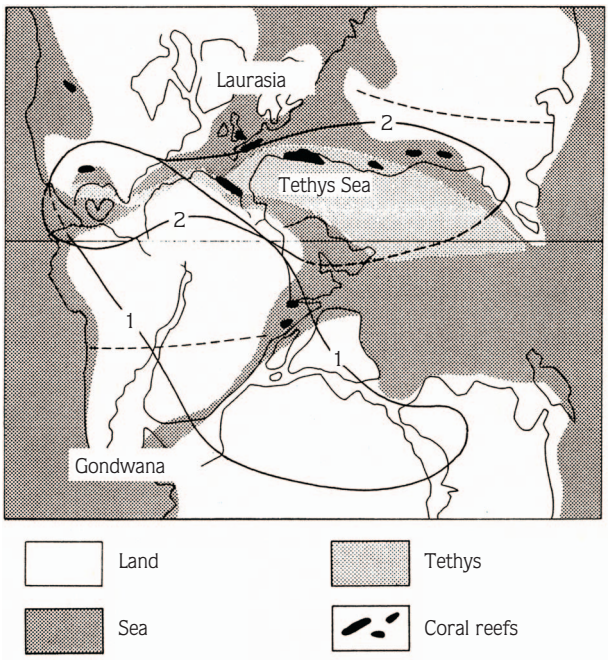

1. Continental xerotherm-Pangaean range
2. Circum Tethyan range

Figure 1. Reconstruction of the land-sea distribution in the Upper Jurassic, with the assumed continental Pangaean area (xerotherm-Pangaean range, 1) and range of the later circum-Tethyan region (2, Old Mediterranean, Mesogean) (from Kürschner, 2000).

At the beginning of the Jurassic, c. 180 million years ago, the breakup of Pangaea started, greatly altering earth's geological history and bryophyte biogeography. The Tethys sea flooded parts of the continents and Laurasia and Gondwana were separated. In addition, the North American continental area was disconnected from the remaining continental dry and arid Pangaean region. These processes and the formation of large mountain systems in the Tertiary resulted in the development of the recent floristic geno-elements and the geographical distribution of the bryophytes. Plant migrations during past geological periods, long-term geological and climatic changes, the recent climate, site conditions, and life strategical structures of the species progenitors, however, have all played a part in the establishment and development of the bryophyte flora and vegetation of South-West Asia.

As a result of these processes, the recent bryophyte flora of South-West Asia is heterogeneous and consists of 6 floral elements that are derived from the different Pangaean ancestral floral stocks (Frey & Kürschner, 1983, 1988; Kürschner, 2000). They clearly reflect earlier processes in palaeogeography and migration. The 6 floral elements are:

- (Sub)cosmopolitan taxa.
- Northern taxa.
- Xerotherm-Pangaean taxa, consisting of an autonomous stock of Pangaean xerophytes.
- Circum-Tethyan taxa that derived from an ancient Mesogean floral stock.
- Tropical taxa with different distribution ranges.
- Endemics of varying origin.

(Sub)cosmopolitan Taxa

(Sub)cosmopolitan taxa are widely distributed in tropical and warm-temperate Europe, Africa, the Americas, Asia, and elsewhere. Their distribution has been widely extended by the activities of man and animal husbandry. Well known examples in the bryophyte flora of South-West Asia, known to all bryologists, are *Anthoceros punctatus* (Anthocerotophyta), *Lunularia cruciata* (L.) Dumort. ex Lindb., *Marchantia polymorpha* L., *Metzgeria furcata* (L.) Corda, *Reboulia hemisphaerica* (L.) Raddi, *Riccia fluitans* L. (Marchantiophyta), *Amblystegium serpens* (Hedw.) Schimp., *Barbula convoluta* Hedw., *Bartramia stricta* Brid., *Brachythecium rutabulum* (Hedw.) Schimp., *B. velutinum* (Hedw.) Schimp., *Bryum argenteum* Hedw., *B. capillare* Hedw., *Ceratodon purpureus* (Hedw.) Brid., *Encalypta vulgaris* Hedw., *Fissidens taxifolius* Hedw., *Grimmia pulvinata* (Hedw.) Sm., *G. trichophylla* Grev., *Gymnostomum calcareum* Nees & Hornsch., *Leptobryum pyriforme* (Hedw.) Wilson, *Platyhypnidium riparioides* (Hedw.) Dixon, *Pohlia cruda* (Hedw.) Lindb., *Polytrichum piliferum* Hedw., *Pseudoscleropodium purum* (Hedw.) M. Fleisch., *Rhytidiadelphus squarrosus* (Hedw.) Warnst., *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr, *Tortula muralis* Hedw., *Trichostomum brachydontium* Bruch, and *Weissia controversa* Hedw. (Bryophyta).

Northern Taxa

The northern element comprises taxa with a former northern Pangaean distribution, i.e. a Laurasian distribution pattern outside the dry and arid parts of North America and the Old World (Schuster, 1983 pro parte; Frey & Kürschner, 1988). Today, taxa of boreal, temperate, sub-Mediterranean, and sub-Atlantic distribution belong to this floral stock.

In South-West Asia the species of northern origin are numerous and concentrate mainly in the northern (Karadeniz Dağları) and southern (Toroslar Dağları) mountains of Turkey, the Iranian mountains (Alborz and Zagros Mts.), Iraq, and North Arabia (Midian, Hijaz, Asir Mts.). In Arabia, most of these species indicate that there was a former western and eastern migration route during the Pleistocene from the mountains of southern Turkey and the Iranian highlands far into the south of the Peninsula, when there was more rainfall (Kürschner, 2000).

Examples of taxa of northern origin are most of the *Barbilophozia* Loeske, *Cephalozia* (Dumort.) Dumort., *Jungermannia* L., *Lophozia* (Dumort.) Dumort., *Porella* L. or *Scapania* (Dumort.) Dumort. species, *Blepharostoma trichophyllum* (L.) Dumort., *Chiloscyphus polyanthus* (L.) Corda, *Frullania dilatata* (L.) Dumort., *F. tamarisci* (L.) Dumort., *Lophocolea bidentata* (L.) Dumort., *Pellia epiphylla* (L.) Corda, *Plagiochila asplenioides* (L.) Dumort. (Marchantiophyta), most of the *Anomodon* Hook. & Taylor, *Brachythecium* Schimp., *Campylium* (Sull.) Mitt., *Dicranum* Hedw., *Eurhynchium* Bruch & Schimp., *Grimmia* Hedw., *Hypnum* Hedw., *Orthotrichum* Hedw., *Plagiomnium* T. J. Kop., *Plagiothecium* Bruch & Schimp., *Rhynchostegium* Bruch & Schimp., or *Schistidium* Brid. species, *Atrichum undulatum* (Hedw.) P. Beauv., *Climacium dendroides* (Hedw.) F. Weber & D. Mohr, *Ctenidium molluscum* (Hedw.) Mitt., *Dicranella varia* (Hedw.) Schimp., *Didymodon vinealis* (Brid.) R.H. Zander, *Eucladium verticillatum* (Hedw.) Bruch & Schimp., *Fissidens dubius* P. Beauv., *Homalia trichomanoides* (Hedw.) Schimp., *Leucobryum glaucum* (Hedw.) Ångström, *Neckera crispa* Hedw., *Palustriella commutata* (Hedw.) Ochyra, *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Sanionia uncinata* (Hedw.) Loeske, *Tetraphis pellucida* Hedw., *Thamnobryum alopecurum* (Hedw.) Nieuwl. ex Gangulee, and *Tortella tortuosa* (Hedw.) Limpr. They are typical components in the understorey of most Euro-Siberian deciduous and evergreen forest formations.

Xerotherm-Pangaean Taxa

The present-day distribution pattern of numerous xerophytes, or 'desert mosses', widely corresponds to a former Permo-Triassic continental Pangaean range (Figure 1). Until the late Mesophytic, this region was an ecological and floristic entity, characterised – at least locally – by arid conditions under which many xerophytes from highly developed progenitors evolved (Schuster, 1981; Frey & Kürschner, 1988). Eco-morphologically, many of these taxa show a strong tendency to establish adaptive structures to tolerate dry periods, which were summarised as 'xeropottioid' and 'xerothalloid life-syndromes' (Frey & Kürschner, 1983; Kürschner & Ghazanfar, 1998). These morphological and physiological adaptations have originated separately by parallel evolution within most of the desert Pottiaceae and thallose Marchantiales.

Today, these xerotherm-Pangaean elements show a very disjunct distribution in the deserts of the northern and southern hemispheres. Typical examples are several thallose Marchantiales, such as *Exormotheca pustulosa* Mitt., *Oxymitra paleacea* Bisch., *Plagiochasma rupestre* (G. Forst.) Stephani, *Riccia lamellosa* Raddi, and *Targionia hypophylla* L., and well adapted Pottiaceae, such as *Aloina rigida* (Hedw.) Limpr., *Crossidium davidai* Catches., *Didymodon australasiae* (Hook. & Grev.) R.H. Zander, *Pterygoneurum ovatum* (Hedw.) Dixon, *Pseudocrossidium replicatum* (Taylor) R.H. Zander, and *Tortula atrovirens* (Sm.) Lindb. It can be assumed that they all derived from this ancient floral stock.

Circum-Tethyan Taxa

Since the breakup of Pangaea, the 3 xerothermic regions of the eastern Holarctic plant kingdom, namely the Mediterranean, Saharo-Sindian, and Irano-Turanian, formed a floristic-historical unit, well-known as the Mesogean region sensu Zohary (1973), or the Old Mediterranean. Together with the arid North American region, the Maderan/Sonoron subkingdom (Takhtajan, 1969), this geno-element mainly consists of marchantioid and riccioid liverworts and acrocarpous mosses, and was distributed along the northern and southern coasts of the Tethys sea (circum-Tethyan subkingdom, Frey & Kürschner, 1983; cf. Figure 1). This element is closely related to the xerotherm-Pangaean flora and today represents a characteristic feature in South-West Asian bryophytes. More than 80 taxa belong to this floral stock (Table 1), which penetrates far into the arid and hyper-arid parts of the Arabian Peninsula, and the deserts of Iran.

Tropical Taxa

In Cretaceous and Tertiary times, a great number of taxa of Gondwanian origin migrated northwards into the circum-Tethyan and Laurasian regions (Schuster, 1981,

Table 1. Taxa of circum-Mediterranean origin in the bryoflora of South-West Asia.

Marchantiophyta

Athalamia spathysii
Cephaloziella baumgartneri
Cephaloziella dentata
Cephaloziella turneri
Fossombronia angulosa
Fossombronia caespitiformis
Gongylanthus ericetorum
Mannia androgyna
Petalophyllum ralfsii
Riccia atromarginata var. *atromarginata*
Riccia atromarginata var. *jovet-astiae*
Riccia crinita
Riccia crozalsii
Riccia glauca
Riccia macrocarpa
Riccia nigrella
Riccia trabutiana
Saccogyna viticulosa
Southbya nigrella
Southbya tophacea

Bryophyta

Acaulon triquetrum
Aloina aloides
Aloina ambigua
Barbula bolleana
Bryum provinciale
Bryum splachnoides
Bryum syriacum
Cheilothela chloropus
Crossidium aberrans
Crossidium crassineve
Crossidium laxefilamentosum
Crossidium squamiferum
Didymodon bistratosus
Didymodon revolutus
Didymodon sicculus
Didymodon umbrosus
Ditrichum subulatum
Encalypta intermedia
Entosthodon attenuatus
Entosthodon fascicularis
Entosthodon muhlenbergii
Fabronia ciliaris
Fissidens arnoldii
Funaria pulchella
Gigaspermum mouretii
Grimmia decipiens
Grimmia orbicularis
Gyroweisia reflexa
Orthotrichum macrocephalum
Phascum cuspidatum
Physcomitrium pyriforme
Pleurochaete squarrosa
Pseudocrossidium hornschuchianum
Pseudocrossidium revolutum
Pterogonium gracile
Pterygoneurum lamellatum
Pterygoneurum ovatum
Pottia commutata
Pottia crinita
Scleropodium cespitans
Scleropodium touretii
Scorpiurium circinatum
Syntrichia caninervis var. *gypsophila*
Syntrichia laevipila
Timmiella anomala
Timmiella barbuloides
Tortella inflexa
Tortella nitida
Tortula brevissima
Tortula cuneifolia
Tortula fiorii
Tortula inermis
Tortula revolvens
Tortula solmsii
Tortula vahliana

1983). Today, they form a striking part of the vegetation within the monsoon-influenced, seasonally more humid escarpment mountains of Arabia and Socotra Island, demonstrating the close relationship of the bryophyte flora to neighbouring Africa, as well as to South-East Asia (Kürschner, 1986, 2000). According to today's distributional range, one can observe:

- Pantropical taxa.
- Taxa with an American-African-South-West Asian range.
- Strictly palaeotropical taxa (e.g., taxa with an African-South-West Asian-South-East Asian distribution pattern).
- Taxa with South-West Asian-South-East Asian/ Oceanian range.
- Widely xero-tropical African taxa.
- Afromontane taxa.

Pantropical Taxa

Several species show a pantropical distribution pattern and often are relicts, which are indicators of former migration routes and the function of South Arabia as a bridge between Africa and Asia (Kürschner, 1986). Long-range dispersal in some cases, however, cannot be excluded with certainty.

Examples of taxa with a pantropical range are *Frullania ericoides* (Nees ex Mart.) Mont., *Lopholejeunea nigricans* (Lindenb.) Stephani, *Mastigolejeunea auriculata* (Wilson & Hook.) Schiffner, *Radula quadrata* Gottsche, *R. volute* Taylor (Marchantiophyta), *Barbula indica* (Hook.) Spreng., *B. tenuirostris* Brid., *Braunia secunda* (Hook.) Bruch & Schimp., *Campylopus pilifer* Brid., *Entodontopsis leucostega* (Brid.) W.R. Buck & Ireland, *Fissidens flaccidus* Mitt., *F. pellucidus* Hornsch., *F. serratus* Müll. Hal., *Gymnostomiella vernicosa* (Hook. ex Harv.) M. Fleisch. var. *tenerum* (Müll. Hal. ex Dusén) Arts, *Hyophila involuta* (Hook.) A. Jaeger, *Palamocladium leskeoides* (Hook.) E. Britton, and *Syntrichia fragilis* (Taylor) Ochyra.

Taxa with an American-African-South-West Asian Range

A few mosses show an American-African-South-West Asian range, and – at present – are not known from South-East Asia. These are *Erpodium glaziovii* Hampe and *Pterogoniadelphus assimilis* (Müll. Hal.) Ochyra & Zijlstra, both frequent in the monsoonal forests of South Arabia.

Strictly Palaeotropical Taxa

Taxa with a strictly palaeotropical range (e.g., taxa with an African-South-West Asian-South-East Asian distribution pattern), lacking in the Neotropics, are frequently associated in Arabia with the drought-deciduous *Acacia* Mill.-*Commiphora* Jacq. and *Sterculia africana* (Lour.) Fiori woodlands. Quite good conditions are also present in the steep wadi cuts dominated by a broad-leaved *Combretum molle* R. Br. ex G. Don -*Dobera glabra* (Forssk.) Poir. riverine forest. Here, they grow on soil, beneath rocks and boulders or in small depressions in the understorey of the forests.

Taxa with this distributional range, for example, include *Cyathodium cavernarum* Kunze, *Fossombronia crispa* Nees, *Plagiochasma eximium* (Schiffner) Stephani, *P. microcephalum* (Stephani) Stephani, *Riccia congoana* Stephani, *R. okahandjana* S.W. Arnell (Marchantiophyta), *Brachymenium nepalense* Hook., *Bryum arachnoideum* Müll. Hal., *Fissidens crispulus* Brid., *F. schmidii* Müll. Hal., *F. sylvaticus* Griff., *Hydrogonium afrofontanum* (Müll. Hal.) Hilp., *Hymenostylium hildebrandtii* (Müll. Hal.) R.H. Zander, *Macrocoma tenuis* (Hook. & Grev.) Vitt, *Micropoma niloticum* (Delile) Lindb., and *Splachnobryum aquaticum* Müll. Hal.

Taxa with a South-West Asian-Southeast Asian/Oceanian Range

A few species show a South-West Asian-South-East Asian/Oceanian distribution pattern, lacking so far from Africa. They often reach the westernmost stands in South Arabia or on Socotra Island. Such relicts, which again are indicators of former migration routes, are *Claopodium prionophyllum* (Müll. Hal.) Broth., *Chionoloma bombayense* (Müll. Hal.) P. Sollman, *Diaphanodon procumbens* (Müll. Hal.) Renauld & Cardot, *Fissidens splachnobryoides* Broth., *Papillaria crocea* (Hampe) A. Jaeger, *Philonotis falcata* (Hook.) Mitt., *Trachycystis ussuriensis* (Maack & Regel) T.J. Kop., and *Tuerckheimia svihlae* (E.B. Bartram) R.H. Zander.

Widely Xero-Tropical African Taxa

Taxa with a wider African-Arabian distribution pattern are *Asterella pappii* (Gola) Grolle, *Frullania schimperi* Nees, *Lejeunea rhodesiae* R.M. Schust., *Marchesinia excavata* (Mitt.) Schiffner, *Microlejeunea africana* Stephani, *Plagiochila fusifera* Taylor, *Radula appressa* Mitt., *R. comorensis* Stephani, *Riccia albolimbata*, *R. argenteolimbata* S.W. Arnell (Marchantiophyta),

Brachymenium leptophyllum (Bruch & Schimp. ex Müll. Hal.) Bruch & Schimp. ex A. Jaeger, *Fissidens bogosicus* Müll. Hal., *F. sciophyllus* Mitt., *Gymnostomiella monodii* P. de la Varde, *Hymenostylium crassinervium* Broth. & Dixon, *Hyophila punctulata* (Mitt.) Kindb., *Philonotis pungens* (Mitt.) Mitt., and *Racopilum capense* Müll. Hal. ex Broth. (Bryophyta). They are widely distributed in a broader belt ranging from West Africa to South Arabia.

Afromontane Taxa

A large stock of palaeotropical taxa belong to the Afromontane element sensu White (1978) and White & Léonard (1991). These high mountain species arrived by migration via the East African mountain chains c. 15-35 million years ago when South Arabia and Socotra Island were linked with the African mainland (Fleitmann et al., 2004). Many of these species are frequently found in the mountains along the Rift Valley, which act as 'stepping stones'. Their total range often includes eastern South Africa, xero-tropical East Africa, Somalia, and the Ethiopian highlands. In Arabia, this Afromontane exclave extends far to the north, including Jabal Ibrahim (Asir Mts.), south of the city of Taif.

Most of these foliose liverworts and pleurocarpous mosses grow as epiphytes in the upper montane forests of Arabia and Socotra Island, and are associated with the *Juniperus procera* Hochst. ex Endl. - *Olea* L.- *Tarchonanthus* L. and *Anogeissus dhofarica* A. J. Scott woodland, and the evergreen Afromontane forests of Socotra Island. They demonstrate, both by their life forms and systematic affinities, the relatively young age of the Afromontane element, which evolved in 'co-evolution' with subtropical and tropical rain forests at the end of the Tertiary.

Typical Afromontane taxa are *Chonecolea ruwenzorensis* E.W. Jones, *Frullania caffraria* Stephani, *F. obscurifolia* Mitt., *F. socotrana* Mitt., *F. trinervis* (Lehm.) Lehm. & Lindenb., *Lejeunea aethiopica* E.W. Jones, *L. capensis* Gottsche, *Plagiochasma beccarianum* Stephani, *Plagiochila squamulosa* Mitt. (Marchantiophyta), *Fabronia abyssinica* Müll. Hal., *F. socotrana* Mitt., *Fissidens megalotis* Schimp. ex Müll. Hal. subsp. *helictocaulos* (Müll. Hal.) Brugg.-Nann., *Leucodon dracaenae* Solms ex Venturi var. *schweinfurthii* (Müll. Hal.) M. Fleisch., *Macrocoma abyssinica* (Müll. Hal.) Vitt, *Pleurochaete malacophylla* (Müll. Hal.) Broth., *Pseudocrossidium porphyreoneurum* (Müll. Hal.) R.H. Zander, *Pseudoleskea leikipia* (Müll. Hal.) Paris, and *P. plagiostoma* Müll. Hal.

Endemic Taxa

The endemic bryophytes of South-West Asia are of different origins. Currently, more than 50 taxa seem to be restricted to the area.

In particular, within the 'desert bryophytes' one can see a complex of evolving taxa of circum-Tethyan and xerotherm-Pangaean origin that grows in the arid and hyper-arid regions of South-West Asia. Examples are *Bryum nanoapiculatum* Ochi & Kürschner (Yemen), *Crossidium deserti* W. Frey & Kürschner (Saudi Arabia), *Crossidium woodii* (Delgad.) R.H. Zander (Yemen), *Entosthodon handelii* (Schiffner) Lazarenko (SW Asia), *Riccia crenatodentata* O.H. Volk (Oman, UAE), *Syntrichia caninervis* Mitt. var. *pseudodesertorum* (Vondr.) M.T. Gallego (SW Asia), *Targionia hypophylla* L. subsp. *linealis* W. Frey & Kürschner (Saudi Arabia), and *Tortula mucronifera* W. Frey, Kürschner & Ros (SW Asia).

Among the Afro-Arabian palaeoendemics one can mention *Fabronia socotrana* Mitt. (Saudi Arabia, Socotra, Yemen), *Fissidens ellipticoides* Brugg.-Nann. & Kürschner (Yemen), *F. laxetexturatus* Brugg.-Nann. (Oman, Yemen), *Schlotheimia balfourii* Mitt. (Socotra), *Sematophyllum socotrense* Buck (Socotra), *Tortella smithii* C.C. Towns. (Socotra), *Weissia artocosana* R.H. Zander (Socotra), and *W. socotrana* Mitt. (Socotra).

Most of the endemics, however, are probably of northern origin. They include the liverworts *Jungermannia handelii* (Schiffner) Amak., *J. lignicola* (Schiffner) Grolle, and *J. subtilissima* (Schiffn.) Grolle from Turkey, as well as various mosses shown in Table 2.

The Tropical Element in the Vegetation of South Arabia (examples)

Before the Arabian Peninsula was separated from the African continent, not earlier than in the Oligocene, East Africa and South Arabia had a common xerotropical flora and vegetation for a long time (Kürschner et al., 2004). Migrations and exchange between the floras were possible from Africa across South Arabia to Asia and vice versa during this time. The aridisation of the entire region in the late Tertiary changed the situation, and the formerly common palaeo-African vegetation was fragmented, isolated, and restricted to several isolated monsoon-affected refuge areas where these relicts survived. These palaeo-African refuge areas today belong to the most interesting areas in South Arabia.

Table 2. Endemic taxa of northern origin in the bryoflora of South-West Asia.

Marchantiophyta

Jungermannia handelii (Turkey)

Jungermannia lignicola (Turkey)

Jungermannia subtilissima (Turkey).

Bryophyta

Brachythecium ehrenbergii (Jordan, Sinai-Peninsula)

Brachythecium umbilicatum (Iran, Sinai-Peninsula, Turkey)

Bryoerythrophyllum compactum (Afghanistan)

Bryum elwendicum (Iran)

Bryum funckiioides (Afghanistan)

Bryum mildeanum (Lebanon, Turkey)

Bryum purpureolucidum (Afghanistan)

Cinclidotus bistratosus (Turkey)

Cinclidotus pachyloma (incl. *C. nyholmiae;* Israel, Lebanon, Turkey)

Fissidens persicus (Iraq, Iran)

Fontinalis mesopotamica (Syria)

Grimmia crassifolia var. *cucullata* (SW Asia)

Hydrogonium heterophyllum (Afghanistan)

Hydrogonium patulifolium (Afghanistan)

Hymenostylium diversifolium (Afghanistan)

Leptodictyum kurdicum (Turkey)

Leucodon immersus (Iran, Syria, Turkey)

Orthotrichum cupulatum var. *bistratosum* (Iraq, Syria, Turkey)

Orthotrichum leblebicii (Turkey)

Orthotrichum rupestre var. *kurdicum* (Turkey)

Palamocladium euchloron (Iran, Turkey)

Philonotos laxitexta (Iran)

Pottia gemmifera (Israel)

Pottia galilaeum (Israel)

Pseudoleskeella laxiramea (Iran)

Rhynchostegiella temeriffae var. *persica* (Iran)

Syntrichia caninervis subsp. *gypsophila* (SW Asia)

Syntrichia rigescens (Israel, Jordan, Sinai-Peninsula)

Syntrichia virescens var. *iranica* (Iran, Jordan)

Tortula demawendica (Iran)

Tortula grandiretis (C Asia, Iraq, Turkey)

Tortula kneuckeri (Sinai-Peninsula)

Tortula subtranscaspica (Afghanistan)

Trichostomum mildeanum (Iran)

Four examples should demonstrate the strong influence of the tropical element in Arabia's bryophyte flora.

Jabal Arays

One of the most outstanding areas in South Arabia is the Jabal Arays, an isolated mountain massif north-east of Aden, rising up to 1716 m. It is characterised by a strong summer-monsoon rainfall that favours, on the sea-facing slopes, the development of a nice *Sterculia africana* (Lour.) Fiori subsp. *arabica* woodland. This woodland, which has close floristic affinities with North-East Africa survived in this refuge area to the present (Kürschner et al., 2006a).

Typical of the understorey of this woodland are volcanic rock outcrops, and temporarily moist depressions, cavities, hollows, and flats, with a very fine soil layer overlying the volcanic rocks. These sites harbour a distinct bryophyte community, which can be seen by the naked eye only after sufficient rainfall, when the soil is wet for a long period. This community was described as Riccietum jovet-astii – argenteolimbatae Kürschner 2003 (cf. Kürschner, 2003a), and consists of several marchantioid and riccioid liverworts with drought-resistant gametophytes. The community forms extensive and compact carpets dominated by several palaeo-African *Riccia* species, such as *R. albolimbata* S.W. Arnell, *R. argenteolimbata* O.H. Volk & Perold, *R. atromarginata* Levier var. *jovet-astiae* Rauh & Buchloh, *R. congoana, R. trichocarpa* M. Howe, the Arabian endemic *R. crenatodentata,* the conspicuous, white-ciliate *Oxymitra incrassata*, *Exormotheca pustulosa,* and *Plagiochasma rupestre*. All are stress-tolerant and well-adapted to the open, sunny, and xeric sites by various ecomorphological adaptations (xerothalloid life-syndrome). Mosses, such as *Crossidium crassinerve* (De Not.) Jur., *C. laxefilamentosum* W. Frey & Kürschner, *Didymodon vinealis* (Brid.) R.H. Zander, *Fissidens schmidii, Gigaspermum mouretii* Corb., and *Pseudocrossidium porphyreoneurum* (Müll. Hal.) R.H. Zander, sporadically occur.

Phytogeographical analysis (Figure 2) indicates a strong xerotropical element in this association. More than 30% of the species belong to palaeotropical, mainly African species, followed by a high proportion of taxa of circum-Tethyan (31.3%) and xerotherm-Pangaean (18.5%) origin. The proportions, however, of the second and third elements are not surprising, as they consist of

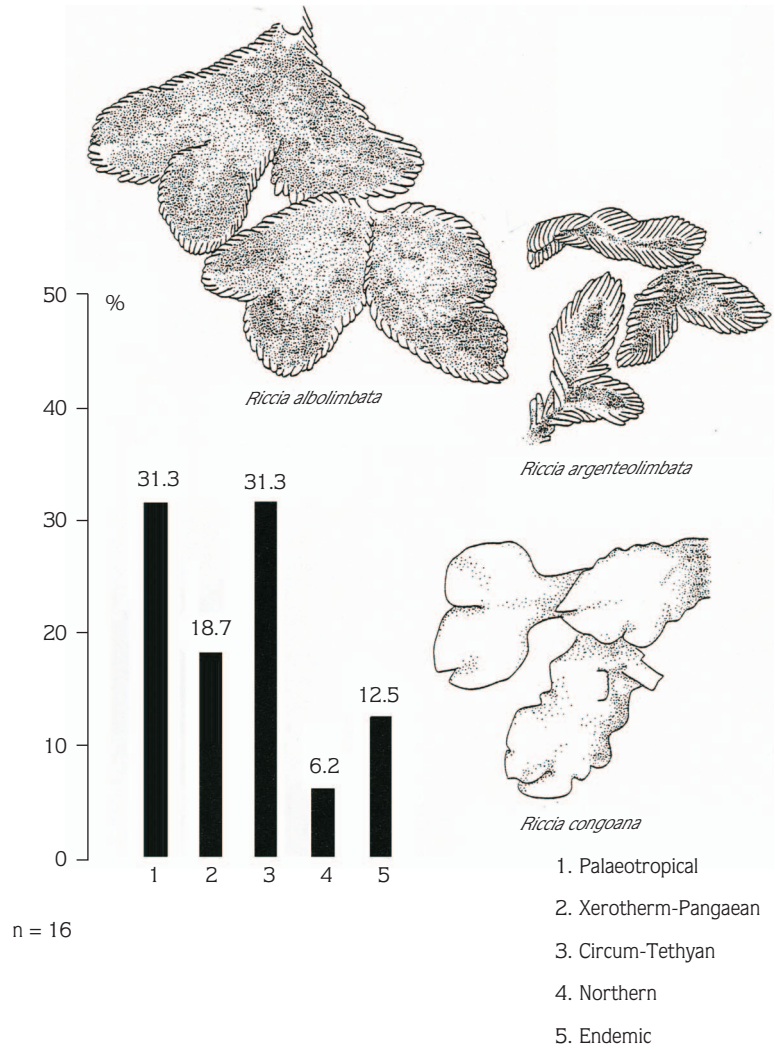

Figure 2. Phytogeographical analysis of the *Riccietum jovet-astii – argenteolimbatae* (Jabal Arays; from Kürschner, 2003a).

highly adapted xerophytes that are widely distributed on the Arabian Peninsula. Remarkable in this community is the high proportion of Arabian endemics (12.5%).

Al-Mahra/Dhofar Mountains

The second example comes from the South Arabian *Anogeissus dhofarica* forests (*Hybantho durae-Anogeissetum dhofaricae* Kürschner et al. 2004) of eastern Mahra/Yemen and Dhofar/Oman. Here again, an outstanding xerotropical refuge area exists, ranging from the 'fog oases' of Jabal Qamar in Dhofar to the Hawf and Fartak Mountains of al-Mahra/Yemen (Kürschner et al., 2004). The strong summer monsoonal rainfalls favour the establishment of dense forests, which are dominated by the endemic Combretaceae *Anogeissus dhofarica.* These species-rich forests are a palaeo-African relict of a former continuous belt of xerotropical forests ranging in the late Tertiary from mainland Asia across South Arabia to Africa (Kürschner et al., 2004).

Frequent in the understorey of these forests are terrestrial bryophytes that form a typical – at present not described – synusium on soil, earthy banks, and amongst boulders. As in the phanerophytes, the bryophytes reflect the strong tropical nature and origin of the forests (Figure 3). Most common are pantropical and

		Oman		Yemen		
	Locality	Jabal Qamar	Uteq	Shah'rut	NW Fartak	E Fartak
	Altitude (m)	500-880	750-900	350-700	750-950	750-780
Taxa of pantropical and palaeotropical range	*Barbula consanguinea*	●	●	●	●	●
	Hyophila involuta	●	●	●	●	●
	Hymenostyliamu crassinervium	●	●	●	●	●
	Plagiochasma beccarianum	●	●	●	●	.
	Pseudocrossidium porphyreoneurum	●	●	●	●	.
	Plagiochasma eximium	●	●	.	●	.
	Fissidens flaccidus	●	●	.	.	.
	Fissidens laxetexturatus	●	●	.	.	.
	Riccia congoana	.	●	●	.	.
	Fissidens schmidii	.	●	.	.	.
	Barbbula indica	.	.	●	.	.
Taxa of northern and circum-Tethyan oriigin	*Weissia condensa*	●	●	●	●	.
	Pleurochaete squarrosa	.	●	.	●	.
	Tortella nitida	.	.	.	●	.
	Didymodon acutus	.	.	.	●	.
	Tortella inflexa	.	.	.	●	●
	Tortella humilis	.	.	.	●	●
	Fossombronia angulosa	.	.	.	●	.
		→ increasing aridity				

Figure 3. Terrestrial bryophyte synusium in the understorey of the *Anogeissus dhofarica* woodland (al-Mahra/Yemen and Dhofar/Oman).

palaeotropical taxa, such as *Barbula consanguinea* (Thwaites & Mitt.) A. Jaeger, *B. indica* (Hook.) Spreng., *Fissidens flaccidus* Mitt., the endemic *F. laxetexturatus* Brugg.-Nann., *F. schmidii, Hyophila involuta* (Hook.) A. Jaeger, *Hymenostylium crassinervium* Broth. & Dixon, *Plagiochasma beccarianum, P. eximium* (Schiffner) Stephani, *Riccia congoana*, and *Pseudocrossidium porphyreoneurum*. Towards the west (Fartak), under decreasing monsoon influence, the tropical element more and more is vanishing, as indicated by a higher proportion of circum-Tethyan xerophytes and northern species. Examples are *Didymodon acutus* (Brid.) K. Saito, *Pleurochaete squarrosa* (Brid.) Lindb., *Tortella humilis* (Hedw.) Jenn., *T. inflexa* (Bruch) Broth., *T. nitida* (Bruch) Broth., and *Weissia condensa* (Voit) Lindb. The latter all have a wider distribution on the Arabian Peninsula.

Phytogeographical analysis (Figure 4) clearly shows the high proportion of tropical species in the understorey of the *Anogeissus* forests. More than 55% of the taxa are tropical species, c. 22% are of circum-Tethyan origin, c. 16% are northern species, and c. 5% are endemics.

Socotra Island

Another example is the epiphytic communities of Socotra Island. Today, the highest parts of the Haghier Mountains on Socotra Island are a hidden and sheltered refugium, very difficult to reach. This refugium preserves a mosaic of evergreen Afromontane forests, woodlands, and heathlands of extraordinary floristic richness, described and classified just recently (*Trichodesmo scottii-Cephalocrotonetum socotrani* Kürschner et al., 2006, *Leucado hagghierensis-Pittosporetum viridiflorum* Kürschner et al., 2006; cf. Kürschner et al., 2006b).

Most of the trunks and twigs in these forests are densely festooned with bryophytes, the occurrence of which was unknown until 2003. This epiphytic bryophyte

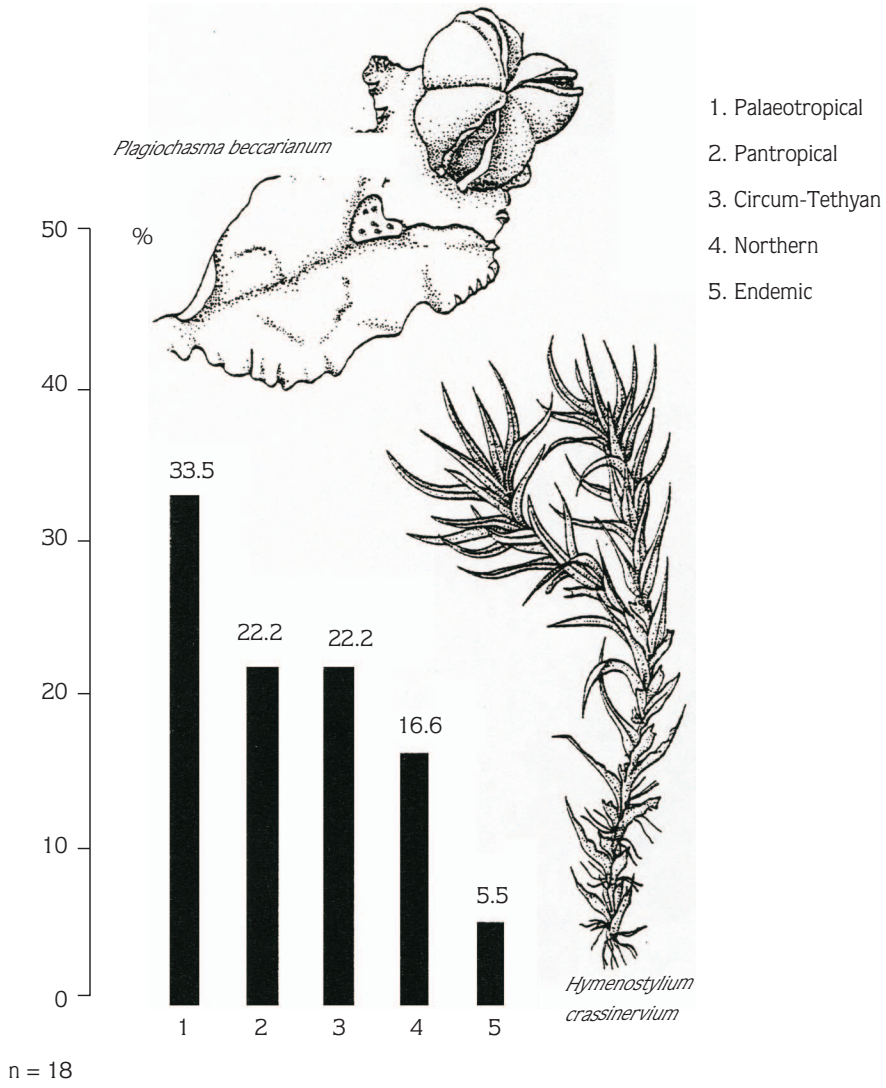

Figure 4. Phytogeographical analysis of the bryophyte synusium in the understorey of the *Anogeissus dhofarica* woodland (al-Mahra/Yemen and Dhofar/Oman).

community, which is dominated by pleurocarpous mosses and liverworts, was described as *Lejeuneo rhodesiae-Sematophylleum socotrense* Kürschner 2004. It is strongly confined to monsoon-affected, foggy, and misty sites. Irradiation and drought-stress here are lowered by daily fog and mist, even in summer (Kürschner, 2004). Character species of the association are the palaeotropical, tiny liverwort *Lejeunea rhodesiae,* the African *Macrocoma abyssinica*, and the Socotran endemic *Sematophyllum socotrense.* Outstanding and most spectacular among the epiphytes, however, is *Papillaria crocea,* a pendant moss, hanging in long garlands and beards from the trees. This South-East Asian tropical element reaches its western known distribution in the forests on Socotra Island (Figure 5). Co-dominant in the association are the Afromontane *Frullania socotrana, F. schimperiana,* and *Marchesinia excavata,* the pantropical, widespread, and predominantly epiphytic *Brachymenium nepalense, Palamocladium leskeoides*, and *Radula quadrata* Gottsche. They all indicate the very humid site conditions and strong tropical influence. In a physiognomic and phytogeographical sense, these forests and epiphytes clearly represent an exclave of the Afromontane belt of North-East Africa (Kürschner, 2004).

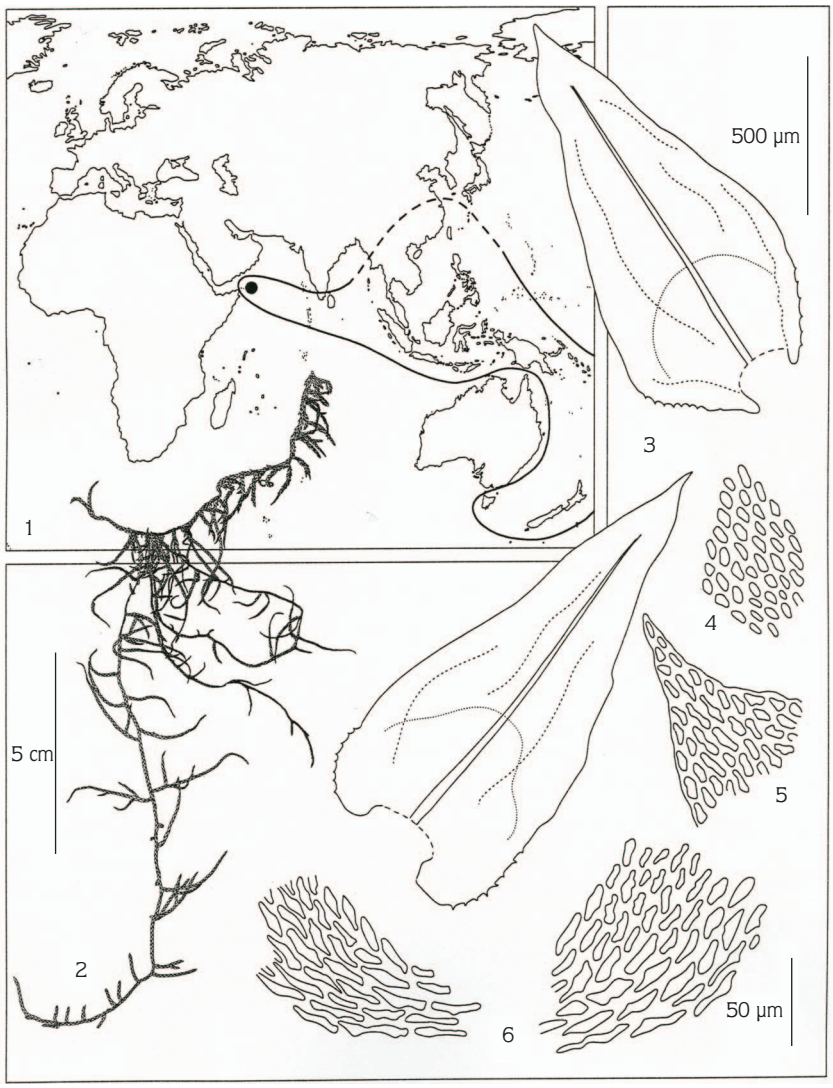

Figure 5. *Papillaria crocea* – 1. Distribution; 2. habit; 3. leaves; 4. mid-leaf cells; 5. leaf tip; 6. basal lamina cells.

The strong tropical influence in Socotra's bryoflora is demonstrated by the phytogeographical analysis of its flora (Figure 6). Nearly 50% of all species are tropical species, whereas taxa of xerotherm-Pangaean, circum-Tethyan, and northern or (sub)cosmopolitan origin are subordinate.

SW Arabia

Epiphytic bryophyte communities, however, also occur on mainland Arabia. Although unexpected plant formations for most bryologists, due to the prevailing desertic climate conditions on the Arabian Peninsula, they can be found in the western and south-western escarpment mountains (Kürschner, 1984, 2003b); yet, as they require a suitable substrate and a certain amount of water in the form of rainfall, fog, or dew, they can exist only under particular site conditions.

In 1984 the first communities were described from the Asir Mountains of Saudi Arabia that form a striking part of the *Juniperis procera* woodland. They are restricted to the highest escarpments that facilitate the penetration of moist air-masses of the summer monsoons. In 2003 these communities were reported also from the south-western Yemeni escarpments (Jabal Eraf; *Leptodonto-Leucodontetum schweinfurthii*

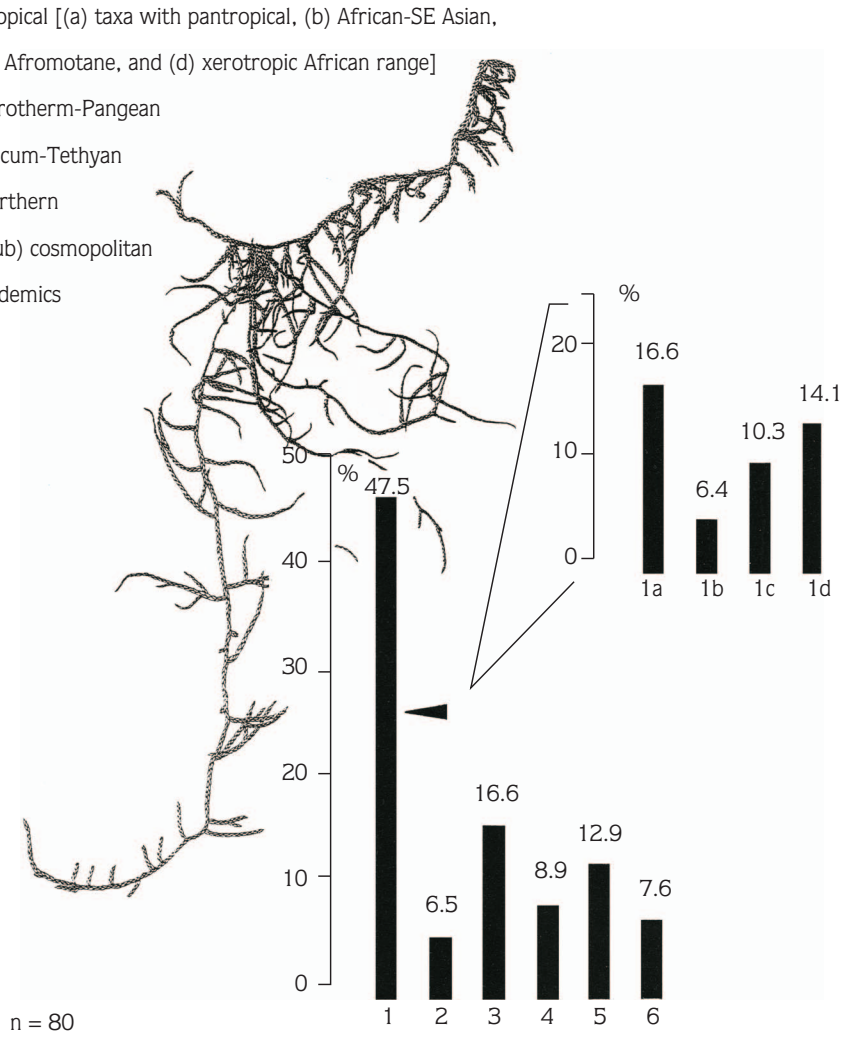

Figure 6. Phytogeographical analysis of Socotra's bryoflora.

Kürschner 2003; *Orthotricho-Fabronietum socotranae* Kürschner 2003).

In particular, the *Leptodonto-Leucodontetum schweinfurthii* is known now from several localities in the western Asir Mountains of Saudi Arabia (e.g., Jabal Ibrahim, Raydah escarpment, Balqarn, Jabal Ashap. J. Sawdah) and from the *Juniperus procera* remnants on Jabal Eraf/Yemen. It is a shade-preferring, humid community dominated by several Afromontane pleurocarpous mosses. In addition, lichens, such as *Anaptychia ciliaris* (L.) Körb., *Usnea articulata* (L.) Hoffm., and *U. bornmuelleriana*, are indicative of high humidity and periodic fog formation.

The phytogeographical analysis of the community, again, clearly demonstrates the Afromontane influence (Figure 7); however, the western migration route for northern and (sub)cosmopolitan species is also indicated by a relatively high proportions (18.2%) of these floral (geno-) elements. They penetrate far into the south of the Arabian Peninsula via the Hjiaz and Asir Mountains.

Summarising Remarks

The analysis of South-West Asia's bryoflora and vegetation indicate that there is a very strong tropical – and especially palaeotropical and Afromontane – influence in the bryophyte flora of the area. This is unexpected and

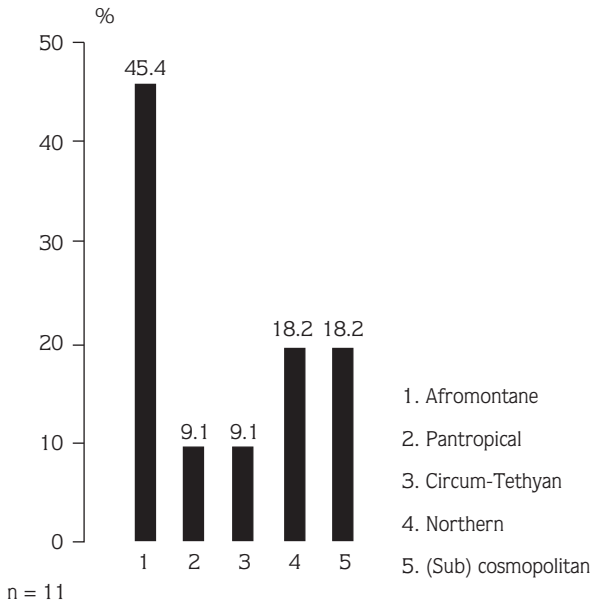

Figure 7. Phytogeographical analysis of the *Leptodonto-Leucodontetum schweinfurthii* (South-Western Arabia).

unknown to many bryologists. Altogether more than 95 taxa, or nearly 10% of South-West Asia's total known bryoflora is of xero-tropical origin. They concentrate mainly in the escarpment mountains of the Arabian Peninsula and – together with the forests and woodlands – often are unique relicts of a former wider distributed Tertiary xero-tropical flora. Today, they link South Arabia with East Africa and South-East Asia.

As many parts of the often inaccessible South Arabian mountain systems still remain unstudied, more taxa can be expected in future; however, during the last 3 decades the area has undergone major changes. The entire region has been developed intensively, leading to a modern infrastructure, which opened up even remote parts of the area. The traditional economy is rapidly transforming, leading to increasing forest destruction and greatly accelerated rural development. As human impact on the forest remnants drastically increases, it is to be feared that many of these remarkable floro-historical elements will vanish or become extinct in the near future.

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